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by

Shane T. Ahyong, Megan L. Porter, and Roy L. Caldwell

A New Species of *Maindronia* Bouvier, 1897 from Iran (Zygentoma: Maindroniidae)

by

Graeme B. Smith, Rafael Molero-Baltanás, Seyed Aghil Jaberhashemi, and Javad Rafinejad

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The Leopard Mantis Shrimp, *Ankersquilla pardus*, a New Genus and Species of Eurysquillid from Indo-West Pacific Coral Reefs

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Abstract. The mantis shrimp superfamily Eurysquilloidea Manning, 1977, with the single family Eurysquillidae Manning, 1977, contains six genera and 32 species, the majority of which occur in the Indo-West Pacific. Here, we describe a new species of eurysquillid, *Ankersquilla pardus*, from the central and western Pacific that cannot be assigned to any recognized genera, and, accordingly, propose a new genus for its reception. *Ankersquilla pardus* is unique in Eurysquilloidea in bearing three teeth on the dactylus of the raptorial claw. Similar raptorial claw armature is otherwise known only in the Parasquilloidea and Pseudosquillidae (Gonodactyloidea). All other eurysquillloids have four or more teeth on the dactylus of the raptorial claw. The most unusual aspect of *Ankersquilla pardus,* however, is the finely spinose posterior abdomen and telson, which resembles members of the Coronididae (Lysiosquilloidea). Although superficially similar to some coronidid lysiosquilloids, the ovate maxilliped 3–4 propodi, ventrally arising intermediate and lateral denticles of the telson, and form of the male pleopod 1 endopod show *Ankersquilla pardus* to be a eurysquilloid.

Introduction

The mantis shrimp superfamily Eurysquilloidea Manning, 1977, with the single family Eurysquillidae Manning, 1977, contains six genera and 32 species, the majority of which occur in the Indo-West Pacific (Ahyong, 2001, Ahyong, 2010; Lucatelli *et al.*, 2013). Eurysquillidae was originally assigned to the Gonodactyloidea Giesbrecht, 1910, based on the ovate maxilliped 3–5 propodi and possession of one or two intermediate denticles on the telson (Manning, 1980; Ahyong, 1997a), but was shown to be outside of the gonodactyloids and instead formed a clade together with the Parasquilloidea Manning, 1995 (also initially thought to be gonodactyloids) and the Squilloidea Latreille, 1802 (Ahyong & Harling, 2000; Van Der Wal *et al.*, 2017). Although highly diverse in telson and uropod ornamentation, eurysquilloids are united by the combination of ovate maxilliped 3–4 propodi and position of the intermediate and lateral denticles of the telson, which arising submarginally on the ventral surface, rather than on the posterior margin (Ahyong & Harling, 2000). Here, we describe a new species of eurysquillid from the western Pacific that cannot be assigned to any currently recognized genera, and, accordingly, propose a new genus for its reception.

Keywords: Crustacea; Stomatopoda; Eurysquilloidea; Eurysquillidae; French Polynesia; Indonesia
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Materials and methods

Morphological terminology and size descriptors generally follow Ahyong (2001, 2012). Specimens are measured in millimetres (mm). Total length (TL) is measured along the dorsal midline, from the apex of the rostral plate to the apices of the submedian teeth of the telson. Carapace length (CL) is measured along the dorsal midline and excludes the rostral plate. The corneal index (CI) is given as 100CL/corneal width. The propodal index (PI) is given as 100CL/propodus length. Specimens are deposited in the collections of the Australian Museum (AM) and Florida Museum of Natural History, University of Florida, Gainesville (UF).

The phylogenetic framework from Porter *et al.* (2010) was used to place the newly described species within known stomatopod taxonomic diversity. New sequences (GenBank accesssion nos: MT062514–MT062516, MT062837–MT062843) for the complete 18S rDNA (c. 2000 bp) and partial 28S rDNA (expansion segments D2–D7b and D9–D10, c. 2800 bp) nuclear genes, and partial 16S (c. 460 bp) and cytochrome oxidase I (COI, c. 650 bp) mitochondrial genes were generated for two specimens of *A. pardus* (AM P102286, P104060) as well as the eurysquilloid species *Manningia pilaensis* De Man, 1902 (AM P100682, Singapore). DNA was extracted from tissues using the NucleoSpin Tissue XS DNA isolation kit (Macherey-Nagel). Polymerase chain reaction (PCR) products for the complete 18S rDNA (c. 2000 bp) and partial 28S rDNA (expansion segments D2–D7b and D9–D10, c. 2800 bp) nuclear genes, and partial 16S (c. 460 bp) and cytochrome oxidase I (COI, c. 650 bp) mitochondrial genes were amplified using one or more sets of general primers as in Porter *et al.* (2010) and Feller *et al.* (2013). Standard PCR conditions (final concentrations in 25µl: 1 × buffer, 200 nmol l^{-1} of each primer, 200 µmol l^{-1} dNTPs and 1 U HotMaster taq from Eppendorf, Hauppauge, NY, USA) were used on a BioRad C1000 Touch Thermal Cycler, with the following cycling parameters: initial denaturation at 96°C for 2 min, followed by 40 cycles of 96°C for 1 min, 46°C for 1 min and 72°C for 1 min, followed by a final chain extension at 72°C for 10 min. PCR products were visualized by agarose gel electrophoresis and purified using the NucleoSpin Extract II kit (Machery Nagel) or ExoSAP-IT (Affymetrix). Sequences were generated in both directions on an ABI PRISM 3500 Automated Capillary Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) using the ABI Bigdye Ready-Reaction kit using 1/16th of the suggested reaction volume. Based on the results of Ahyong & Jarman (2009), Porter *et al.* (2010) and Van Der Wal (2017), which inferred Hemisquillidae (Gonodactyloidea) to be the sister group to the remaining extant stomatopods, we rooted the analysis to *Hemisquilla australiensis* Stephenson, 1967 and *H. californiensis* Stephenson, 1967. Nucleotide sequences of the 16S, 18S and 28S genes were aligned with the online MAFFT server using the E-INS-I strategy (http://mafft.cbrc.jp/alignment/server/) (Katoh *et al.*, 2002; Katoh *et al.*, 2005). The COI sequences were inspected for evidence of pseudogenes (e.g., stop codons, indels not contiguous with codons) and then manually aligned using the translated amino acid sequences. Phylogenetic analyses of combined datasets can reveal hidden support for relationships in conflict among analyses of individual markers (Gatesy *et al.*, 1999); therefore, the four gene regions were concatenated, and highly divergent and/or ambiguous regions of the entire alignment were removed using the program GBlocks (Castresana, 2000). The phylogeny was reconstructed using RaxML (Stamatkis *et al.* 2005; Stamatkis *et al.* 2008; Pfeiffer & Stamatkis 2010) as implemented in the CIPRES portal (Miller *et al.* 2010).

Systematics

Stomatopoda

Eurysquilloidea Manning, 1977

Eurysquillidae Manning, 1977

Ankersquilla gen. nov.

http://zoobank.org/NomenclaturalActs/3724004A-0FF7-41CC-8CB3-6A213641E825

Type species. *Ankersuilla pardus* sp. nov.

Diagnosis. Cornea bilobed, set transversely on stalk, with 6 mid-band rows of ommatidia. Rostral plate simple, apex rounded. Antennular somite not elongated, shorter than twice length of rostral plate. Raptorial claw dactylus with 3 teeth on occlusal margin; propodus occlusal margin fully pectinate; carpus with single dorsal spine. Pleopod 1 endopod with lateral lobe on distal 'endite'. Body dorsoventrally flattened. Abdominal somites 5–6, telson and proximal surface of uropodal protopod densely spinose, obscuring dorsal sculpture. Telson transversely ovate, wider than long, primary spines short, acute, dorsal outline obscured by dorsal spination of telson; submedian denticles absent; intermediate and lateral denticles without dorsal lobe. Uropodal protopod inner primary spine longer than outer; inner margin spinose.

Etymology. Named after Arthur Anker, our friend and colleague who collected the type material. Gender: feminine.

Ankersquilla pardus sp. nov.

http://zoobank.org/nomenclaturalActs/0BD75B46-0194-43AD-A2E9-049982C56C18

Figs 1–4

Holotype: UF23346, ♂ (TL 52 mm), Moorea [French Polynesia], NW side of Cook Bay, off Gump station, 17°29.406'S 149°49.578'W, back-reef, sandy reef flat with massive coral blocks and rubble, 1 m, deep in sand under large piece of rubble, fcn BMOO-6054, sta BIZ 5, coll. A. Anker, 17 October 2009. **Paratype**: AM P102286, ♀ (TL 53 mm), Moorea, SW coast, lagoon off Nihimaru estuary, 17°31.998'S 149°54.306'W, back-reef, sandy reef flat with massive corals, algae and rubble, deep under large algae-covered piece of rubble, 1.5 m, fcn BMOO-4918, sta MIB 167, coll. A. Anker, 29 October 2008.

Other material examined. AM P104060, 1 female (TL 82 mm), Indonesia (probably Bali), purchased, aquarium trade, July 2006.

Description. Eye subtriangular, extending almost to end of or slightly beyond antennular peduncle article 1; cornea strongly bilobed, set transversely on stalk, with 6 mid-band rows of ommatidia; CI 419–501. Ophthalmic somite anterior margin transverse; ventral surface with blunt spine arising proximally and minute distomedian granule. Ocular scales triangular, separate, anterior margins concave, apices directed laterally.

Antennular peduncle 0.58–0.71CL. Antennular somite dorsal processes directed anterolaterally, apices blunt. Antennal protopod dorsally unarmed; with small ventrodistal spine and 1 ventral papilla. Antennal scale length 0.58–0.61CL.

Rostral plate linguiform to subtriangular, slightly

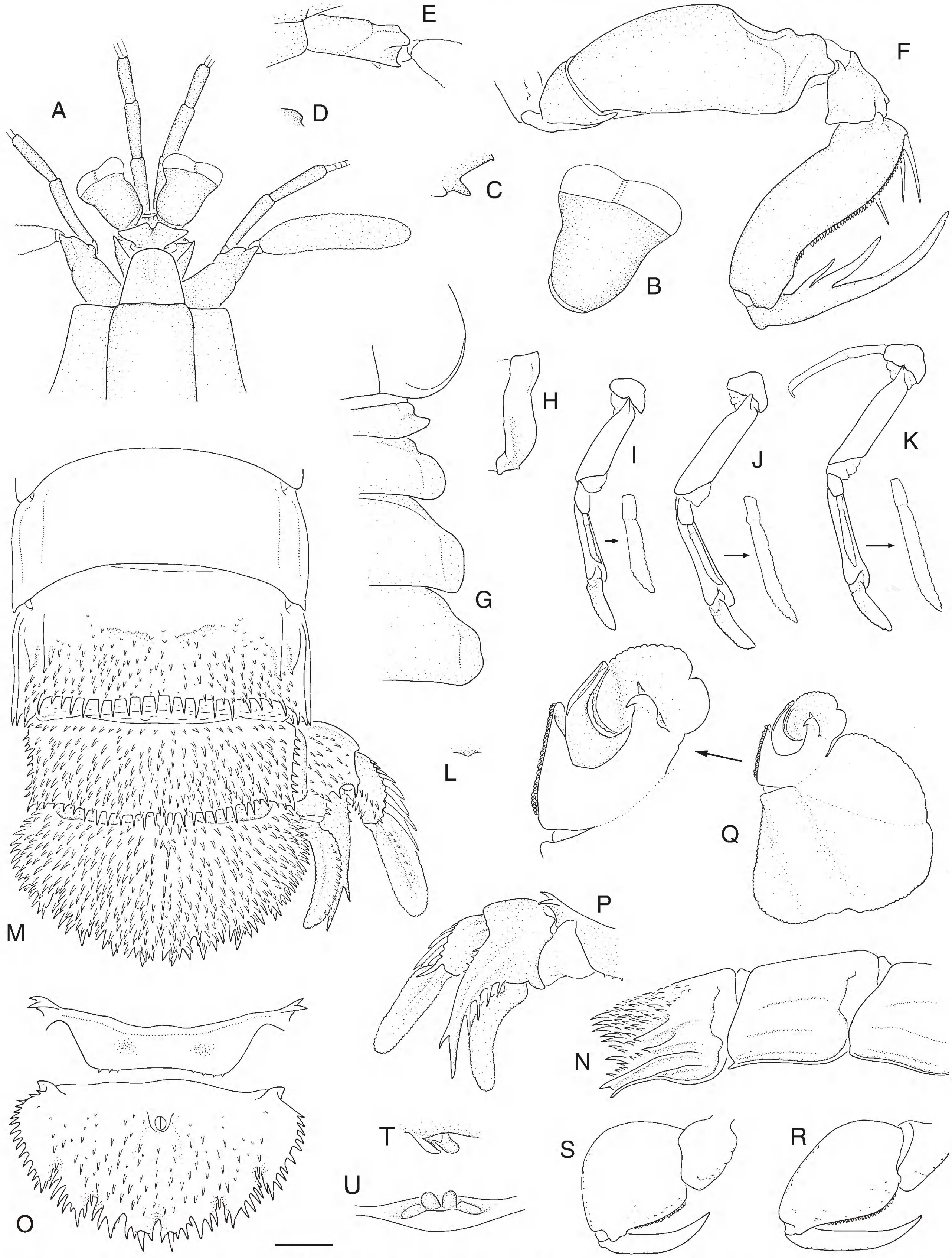

Figure 1. *Ankersquilla pardus* gen. et sp. nov. *(A–S)* male holotype, TL 52 mm, Moorea, UF23346. *(T–U)* female paratype, TL 53 mm, Moorea, AM P102286. *(A)* anterior cephalothorax, dorsal view; *(B)* right eye, dorsal view; *(C)* ventral spine and ventral margin of ophthalmic somite, right lateral view; *(D)* right dorsal process of antennular somite, lateral view; *(E)* right antennal protopod; *(F)* right raptorial claw; *(G)* posterolateral portion of carapace and thoracic somites 5–8, right dorsal view; *(H)* thoracic somite 5, right lateral view; *(I–K)* right pereopods 1–3, posterior view; *(L)* thoracic somite 8, sternal 'keel'; *(M)* abdominal somites 4–6, telson and right uropod, dorsal view; *(N)* abdominal somites 3–5, right lateral view; *(O)* abdominal somite 6 and telson, ventral view; *(P)* right uropod, ventral view; *(Q)* right pleopod 1 endopod; *(R, S)* right maxillipeds 3–4 dactylus–carpus; *(T, U)* female gonopore, right lateral view and ventral view. Setae omitted. Scale = A, C–K, M–P = 2.0 mm; B, L, Q, R–U = 1.0 mm.

Figure 2. *Ankersquilla pardus* gen. et sp. nov. *(A–C)* female, TL 82 mm, Indonesia, AM P104060: eye, telson and right lateral habitus, respectively. *(D)* female paratype, TL 53 mm, Moorea, AM P102286; *(E)* male holotype, TL 52 mm, Moorea, UF23346. (Photos: *A–C,* R. Caldwell; *D–E,* A. Anker).

wider than long, widest basally, lateral margins straight, convergent, apex rounded; low, indistinct median carina. Carapace anterolateral angles bluntly angular, anterior margins straight; carinae absent except for marginal carina, indicated posterolaterally.

Mandibular palp 3-segmented. Maxillipeds 1–5 with epipod. Maxillipeds 3–4 propodi ovate, rounded, without distoventral ribbing. Maxilliped 5 basal article without ventrally directed spine.

Raptorial claw dactylus with 3 teeth; outer margin very weakly sinuous on proximal half, curving distally, with distinct basal notch. Propodus with 3 movable spines proximally, distal margin unarmed; distal margin unarmed; propodus shorter than carapace, when folded, not extending posterior beyond merus; PI 105 (male), 109–120 (female). Carpus dorsal margin terminating in short, ventrally directed spine. Merus inferodistal margin rounded, unarmed. Ischium shorter than one-fourth merus length. Basis lateral surface with 2 or 3 short denticles.

Pereopods 1–3 proximal-most article with outer ventrolaterally directed triangular lobe; inner margin unarmed. Endopod distal article slender, liguliform, tapering distally; outer and inner distal margins setose.

Thoracic somite 5 lateral process obsolete, with small ventrally directed spine. Thoracic somites 6–8 lateral process rounded to subtruncate; faintly indicated lateral carina.

Thoracic somite 6 female gonopore with bilobed median papillae flanked by lower lateral papilla. Thoracic somite 8 sternal keel low, rounded.

Male pleopod 1 endopod with lateral lobe on distal 'endite'.

Abdominal somites loosely articulated; somites 1–4 smooth dorsally; posterior margin unarmed; 3 shallow grooves laterally (upper two corresponding to intermediate and lateral carina) and marginal carina; somites 1–3 posterolaterally unarmed; somite 4 with posterolateral spine; ventral pleural margin straight to faintly concave. Abdominal somite 5 with posterior half to two-thirds covered with short posteriorly directed spines; posterior margin lined with posteriorly directed spines; laterally with 3 posteriorly armed carinae (first and third corresponding to intermediate and lateral carinae) and posteriorly armed marginal carina; ventral pleural margin distinctly concave. Abdominal somite 6 surface entirely covered with short posteriorly directed spines; posterior margin lined with posteriorly directed spines; lateral carina indicated, lined with spines; 2 triangular spines anterior to uropodal articulation, apices simple or bifid (in largest specimen); sternum posterior margin unarmed medially, with 3–10 small spines on each posterolateral margin.

Telson length half width, dorsal outline evenly curved; dorsal surface and posterior margin densely covered with short, curved spines; median carina indicated by longitudinal row of short, curved spines of similar size to adjacent spines on telson surface; submedian teeth short, margins spinose, movable apices conical, curved, separated by narrow, U-shaped cleft; submedian denticles absent; with single spiniform submarginal intermediate and lateral denticles, dorsal lobe absent. Intermediate and lateral teeth short, stout, spinose, not produced beyond general posterior telson outline. Ventral surface covered with short spines; postanal carina absent.

Uropodal protopod dorsal surface covered with short spines; anterior margin convex, unarmed; inner primary spine ventrally carinate, distinctly longer than outer spine; inner margin with 3–5 graded spines; outer margin with 4–11 short spines, unarmed anterior to endopod articulation. Uropodal exopod proximal segment dorsal surface with patch of short spines on inner half; inner margin concave, unarmed; slender, curved distoventral spine; outer margin with 7 or 8 graded movable spines, distalmost not reaching beyond midlength of distal segment. Exopod distal segment longer than proximal segment; dorsal midrib with 7–11 short spines; ventral midrib with 0–3 minute spines. Endopod elongate, reniform, apex bluntly rounded; length 4.57–4.67 × width; dorsolateral surface with row of 10–15 short spines.

Colour in life (Figs 2, 3). Overall pale yellowish-tan with diffuse whitish mottling and numerous black or black-brown spots over cephalothorax, abdomen, tailfan and pereopods, forming leopard-spotted pattern. Eyes pale yellow-tan; cornea silver. Antennular and antennal peduncles with diffuse white speckling; antennular articles distally yellow-brown. Antennal protopod pale with black-brown spots; scale speckled white with dark, irregular patch slightly proximal to midlength and at distal end. Raptorial claw propodus and carpus translucent white and diffuse irregular brown mottling and diffuse blue-green highlights; movable propodal spines translucent white overall (TL 52–53 mm) to black-green on proximal two-thirds (TL 82 mm); dactylus translucent white teeth margined with orange-brown; ischiomerus pale yellowish-tan with diffuse white mottling and several dark diffuse spots, distal margin diffuse blue-green. Uropodal exopod distal article and endopod distal half dark-brown; marginal setae dull-pink.

Figure 3. *Ankersquilla pardus* gen. et sp. nov., lagoon patch of *Halimeda* algae on sand in about 8 m of water at Kwajalein Atoll, Marshall Islands, 27 August 2012. Photo: S. Johnson. Specimen not collected.

Etymology. Derived from the formal name of the Leopard, *Panthera pardus* (Linnaeus, 1758), for the distinctive, leopard- spotted colour pattern of the new species; used as a noun in apposition.

Measurements. Male (n = 1) TL 52 mm; female (n = 2) TL 53–82 mm. Other measurements of holotype: CL 9.0 mm, antennular peduncle length 6.4 mm, antennal scale 5.2 mm, propodus length 8.3 mm, abdominal somite 5 width 10.3 mm.

Habitat. The French Polynesian specimens were collected from shallow (1–1.5 m) sandy back-reef sites with rubble and algae; both were burrowed beneath coral boulders. The Marshall Islands individual was photographed at 8 m depth at Kwajalein Atoll in a lagoon patch of *Halimeda* sp. on sand. The precise collecting locality of the TL 82 mm Indonesian specimen is not known, but in 2000, RLC and Mark Erdmann observed but failed to capture another Indonesian individual in Tolitoli Bay, Sulawesi, dwelling in a large worm tube in massive coral head at 2 m depth.

Distribution. Central to western Pacific, from French Polynesia, the Marshall Islands and Indonesia.

Discussion

Ankersquilla gen. nov., represented by *A. pardus* sp. nov., is unique in Eurysquilloidea in having three teeth on the dactylus of the raptorial claw; all other eurysquillids have four (*Manningia* Serène, 1962; *Coronidopsis* Hansen, 1926) or more dactylar teeth (*Eurysquilla* Manning, 1963; *Eurysquilloides* Manning, 1963; *Raysquilla* Ahyong, 2000; *Sinosquilla* Liu & Wang, 1978) (Ahyong, 1997b, 2001). Three spearing teeth on the dactylus of the raptorial claw are otherwise present only in members of the Parasquilloidea and in Pseudosquillidae Manning, 1977 (Gonodactyloidea). Another unusual feature of *Ankersquilla* is the absence of upright rounded lobes associated with the intermediate and lateral denticles of the telson; these lobes are present in all other eurysquillids except for *Eurysquilloides* Manning, 1963 (Ahyong & Harling, 2000; Ahyong, 2001). Perhaps the

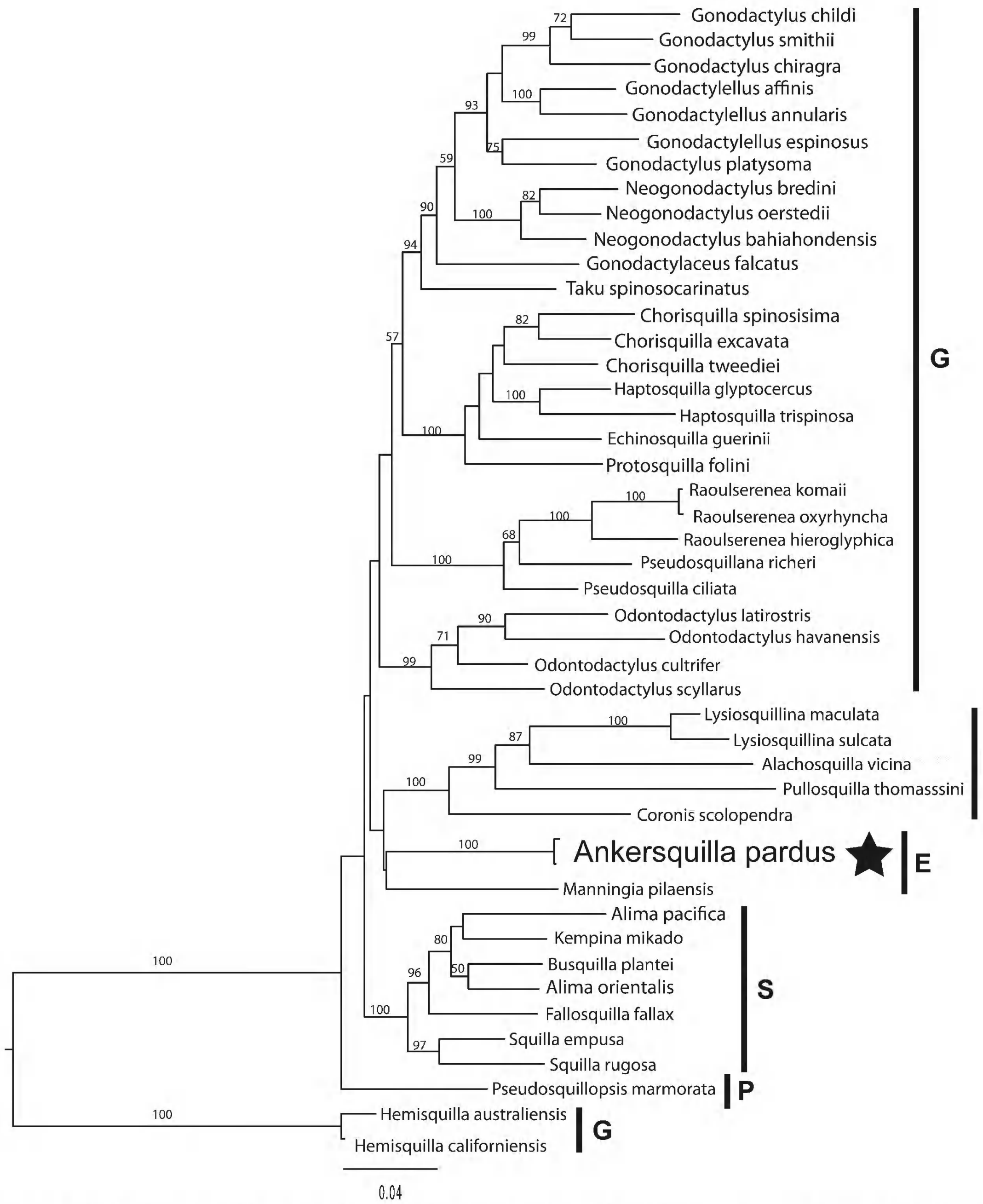

Figure 4. Phylogenetic position of *Ankersquilla pardus* gen. et sp. nov. based on maximum likelihood analysis of concatenated 18S, 28S, 16S, COI sequences using RaXML. Log likelihood -31189.005. Bootstrap support indicated on branches. Superfamily abbreviations: Eurysquilloidea *(E)*, Gonodactyloidea *(G)*, Lysiosquilloidea *(L)*, Parasquilloidea *(P)*, Squilloidea *(S)*.

most remarkable aspect of *Ankersquilla* is its resemblance to some members of the Coronididae Manning, 1980, in the superfamily Lysiosquilloidea Giesbrecht, 1910. The uniformly and densely spinose surface of abdominal somite 6 and the telson of *Ankersquilla*, with a wide, semi-circular telson having short primary teeth resemble the condition in the coronidid genus, *Neocoronida* Manning, 1976. This resemblance between the two genera is further accentuated by the simple, unarmed rostral plate, wide ocular scales, subtriangular eyes and strikingly similar uropod structure (compare Fig. 1M, P with Manning, 1972: fig. 1e, g). Although *Ankersquilla* is clearly not a lysiosquilloid, as indicated by the simple and ovate, rather than ribbed, quadrate propodi of maxillipeds 3–4, and eurysquilloid-form male pleopod 1 endopod (Ahyong & Harling, 2000), it should not be assumed that the similarities to *Neocoronida* are the result of convergence. The maxilliped 3–4 propodi of *Neocoronida* also lack ventral ribbing (Manning, 1976; Adkison *et al.*, 1983) and the intermediate and lateral denticles of the telson are ventrally recessed, as in eurysquilloids. Thus, *Neocoronida* could instead prove to be a eurysquilloid rather than lysiosquilloid, but further assessment of other members of the Coronididae are required prior to making formal changes to the classification. Also, of possible phylogenetic significance is that the two eurysquilloid exemplars form a clade that is placed closer

to the lysiosquilloids (Fig. 4) than to the squilloids and parasquilloids as indicated by previous analyses (Ahyong & Harling, 2000; Van Der Wal *et al.*, 2017). Nodal support for the eurysquilloid-lysiosquilloid affinity is low (as are the relationships between other superfamilies), but such a relationship, if corroborated, would indicate that the dorsoventrally flattened and generally loosely articulated body form shared by most members of Eurysquilloidea and Lysiosquilloidea could be synapomorphic rather than convergent.

Most eurysquilloids have variously spinose posterior abdominal somites and telson, but the surface sculpture and telson outline is not usually obscured as it is in *Ankersquilla*. Also, the median carina of the telson in *Ankersquilla*, which is distinct in most eurysquilloids, is instead indicated only by a longitudinal row of spines of similar size to the surrounding telson spines. Among eurysquilloids, similarly unusual abdominal and telson ornamentation is approached only in *Sinosquilla*. Both species of *Sinosquilla* have dense dorsal spination on abdominal somite 6 and the telson, which largely obscures surface sculpture (Ahyong, 2001: fig. 16; 2010: fig. 1C, D). In *Sinosquilla sinica* Liu & Wang, 1978, the median carina of the telson is distinct and unbroken, but in *S. hispida* Liu & Wang, 1978, the overall dorsal spination is more uniform (albeit more pronounced) and the median carina of the telson is indicated by a row of spines, much like that of *A. pardus*. *Ankersquilla* and *Sinosquilla*, however, are otherwise dissimilar and probably not closely related, being readily separated by numerous features including: three teeth on the dactylus of the raptorial claw in *Ankersquilla* (eight or more in *Sinosquilla*); a short, rounded rostral plate in *Ankersquilla* (long, spiniform in *Sinosquilla*); intermediate and lateral telson denticles without upright lobes in *Ankersquilla* (lobes present in *Sinosquilla*); and short, spiniform intermediate and lateral primary telson teeth that in *Ankersquilla* do not extend beyond the general dorsal outline (prominent, lobe-like in *Sinosquilla*). The phylogenetic position of *Ankersquilla* within the eurysquilloids is presently unclear and awaits comprehensive revision and analysis of all genera (currently underway).

The Indonesian specimen of *A. pardus* (TL 82 mm; AM P104060; Fig. 2A,C) survived in captivity for approximately six and one half years during which it regularly moulted but remained essentially the same size, suggesting that it had already attained maximum length. In captivity this animal fed on shrimp and crabs, but did not break open snails and hermit crabs. Despite their wide geographic separation, the Indonesian specimen of *A. pardus* agrees closely with the smaller French Polynesian type specimens (TL 52–53 mm), differing chiefly in the more tapering rostral plate, blunter dorsal telson and abdominal spines, more numerous short spines overall (most notably those of abdominal somite 5 covering the posterior two-thirds instead of half), and slightly greater spination along the lateral margin of the uropodal protopod (11 versus 4–8) and posterolateral margins of the abdominal sternite 6 (7–10 versus 3–5). These differences are probably a function of the much larger size of the Indonesian specimen (TL 82 mm versus TL 52–53 mm). Evidently, *A. pardus* has strong dispersal capabilities given the low (1%) COI sequence divergence between Indonesian and French Polynesian specimens.

The distinctive coloration of *A. pardus* is consistent in all of the specimens examined, including the individual observed but not captured in Tolitoli Bay, Indonesia (see Habitat above). We identify an individual from the Marshall Islands (photographed but not captured; Fig. 3) as *A. pardus* based on the visible morphology and the distinctive colour pattern. Although common names are seldom used for stomatopods, we here propose Leopard Mantis Shrimp for *A. pardus*, given its distinctive colour pattern.

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A New Species of *Maindronia* Bouvier, 1897 from Iran (Zygentoma: Maindroniidae)

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Abstract. A new species of the genus *Maindronia* Bouvier is described from a single female specimen collected in Iran. It appears close to *M. mascatensis* Bouvier but displays a distinct chaetotaxy compared to that illustrated by earlier authors. The morphology of the species is described in line with current standards including information on the notal trichobothria and the specialized sensilla of the antennae and palps.

Introduction

Bouvier (1897) described an unusual silverfish *Maindronia mascatensis* from six specimens collected by M. Maindron, near Muscat in Oman (Fig. 1), noting that the species shared characters of both the Nicoletiidae Lubbock, 1873 (lacking scales) and the Lepismatidae Latreille, 1802 (the presence of eyes). Escherich (1905) examined one of Bouvier's six specimens and expanded on the description, believing *Maindronia* represented a distinct and separate lineage to the other known families. Escherich's written description lacked much detail but he did provide four illustrations from which additional information can be derived, assuming they are accurate. Wygodzinsky (1940) described a second species *Maindronia neotropicalis* from Chile and Schremmer (1964) described a third, *Maindronia beieri* from Sudan. Wygodzinsky (1962) recorded *Maindronia mascatensis* from a locality in Afghanistan and commented that he was preparing a revision on the subfamily Maindroniinae Escherich, 1905, which unfortunately was never published. Here we describe a new species from a single female specimen collected in Iran. We have been unable to locate the six type specimens of *M. mascatensis*. One of these had been sent to Escherich (most of whose material has been lost), while the other five were supposedly in the Museum national d'Histoire naturelle, however these have not been found there (pers. comm. Markus Koch, 2018). They may have been transferred by Wygodzinsky to Buenos Aires or eventually to New York to facilitate his planned revision. While clear differences between the current specimen and the Escherich illustrations are present we have some doubt as to the accuracy of those illustrations. We also have little understanding of the intra-specific variability of species within this seldom collected family. Nevertheless, we have decided to describe this species as new, anticipating that the types of *M. mascatensis* if or when eventually found, will affirm this decision.

Keywords: Thysanura; taxonomy; new species
Taxonomic registration: (LSID publication) http://zoobank.org/E39C144E-8773-40E0-8855-15BED9363BFD
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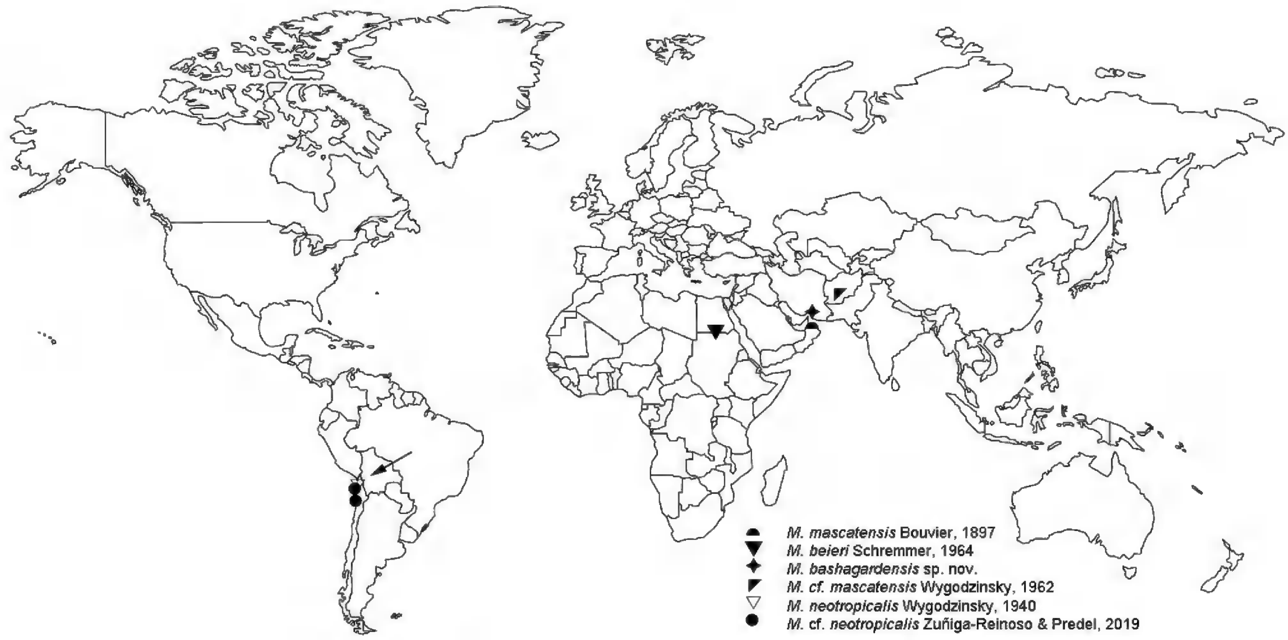


Figure 1. Currently known distribution of *Maindronia* spp.

Materials and methods

The specimen was collected and placed into 100% ethanol. Locality co-ordinates were taken using a hand held Garmin eTrex®20 GPS. A mesothoracic leg was removed and retained in 100% ethanol and stored at 4°C to allow later DNA sequencing. The specimen was then transferred to 80% ethanol for about two months to allow it to soften. Pigment pattern was recorded and the specimen measured and prepared using the methods outlined in Smith (2013). Due to its large size, the dissected specimen was mounted on four slides (head and nota, legs and sterna, urotergites and urosternites I–VI, and the remainder) using Tendeiro medium; tissue was collected during dissection and stored in 100% ethanol for later DNA sequencing. Drawings were made with the aid of an Olympus CX31 binocular microscope fitted with a U-DA drawing attachment. One antenna and a cercus were not mounted on slides but sent to Córdoba for scanning electron microscopy. As previously reported with larger specimens of the Nicoletiidae (Smith *et al*., 2012; Molero *et al*., 2013) the Tendeiro medium had a distorting effect on many of the macrochaetae, although not enough to interfere with an interpretation of the chaetotaxy. Macrochaetae have been illustrated here without showing the change in surface texture visible on the slide mounted material.

The antenna and the cercus used for scanning electron microscopy were put through an ethanol dehydration series finished with hexamethyldisilazane (see Molero *et al*., 2013) and coated with gold with a sample coater BAL-TEC SCD- 005. They were imaged using a microscope JEOL JSM 7800F.

Roman numerals are used to indicate abdominal segment number. The following abbreviations are also used: asl: above sea level (in metres); AMS: Australian Museum, Sydney; HW: head width (in millimetres); H+B: head and body length (in millimetres); L/W: length to width (ratio); PI, PII, PIII: legs of pro-, meso- and metathorax respectively; SEM: scanning electron micrograph; UCO: University of Córdoba.

Illustrations are fairly accurate for the macrochaetae and larger setae but the detail of the smaller setae and cilia is generally only indicative to give an idea of the length and type of bristle. Antennal segmentation uses the terminology introduced in Smith (2015) i.e. *annulus* for the smallest individual unit, *interval* for the collection of annuli forming a repeated pattern where the most distal annulus usually carries trichobothria and is referred to as a *T-annulus*. Nomenclature of the type of antennal sensilla follows that of Adel (1984). In previous work the first author used the term rosette when referring to the ring of chaetic sensilla (setae) around the circumference of each annulus of the antenna or terminal filaments. To avoid confusion with the rosette-like structures of Matushkina (2010), found on the antennae of many Zygentoma and Archaeognatha, this chaetotaxy will here be referred to as rings (of setae).

Systematics

Family Maindroniidae Escherich, 1905

Maindronia Bouvier, 1897

Maindronia bashagardensis sp. nov. Smith & Molero-Baltanás

http://zoobank.org/NomenclaturalActs/2F101CAF-9940-4E93-9C0B-75EECCE185F4

Figs 2–41

Holotype ♀ IRAN: Hormozgan Province, Bashagard County, Jakdan village, 26.4334°N 57.1747°E, 13.vi.2013, Seyed Aghil Jaberhashemi and colleague, collected on porcelain tiles inside rooms; K.541546 (head and nota), K.541546.001 (legs and sterna), K.541546.002 (abdominal segments I–VI), and K.541546.003 (abdominal segments VI–X and terminalia); in the Australian Museum, Sydney.

Diagnosis. Distinguished from *M. mascatensis* by the presence of two combs on the inner process of coxites VIII (versus one), three combs on each coxite VII (versus two) and 4+4 combs on the face of urosternites III–VII (versus 3+3). *Maindronia neotropicalis* lacks dorsal chaetotaxy and *M. beieri* Schremmer, 1964 has only seven pairs of styli and the chaetotaxy appears to be less dense than in the new species.

Description

Appearance: Very large silverfish (Fig. 6), body elongate with parallel sides, dorsoventrally flattened, thorax only slightly wider than abdominal segment I, the following abdominal segments remain about the same width up until the fifth segment after which they slowly taper posteriorly to about 80% the width of the thorax. Eyes almost black. Scales absent but some areas of dark pigmentation as described below.

Body size: H+B length 16.5 mm, thorax width 2.3 mm; antennae incomplete 16.9 mm (a little longer than H+B) and terminal filaments incomplete 11.0 mm (⅔ H+B).

Cuticle and pigmentation: Surface of body, flagellum, legs and styli with tessellated appearance with scattered small setae (Fig. 7), cuticle without tessellated appearance on pedicel and scape, palps, tail filaments and ovipositor. Cuticular pigment blotchy, dark brown or deep purple. Pigment faded noticeably over several days after the specimen was mounted in Tendeiro medium. Antennae and terminal filaments without pigmentation. Head with pigment behind the eyes and along the lateral margins, with a weakly pigmented star-shaped region over much of the vertex, 3+3 distinct but small dark pigment patches occur on either side of the groove between the anterior bushes of macrochaetae and out towards the lateral margins as well as patches along the posterior margin of the vertex; a line of pigment on the dorsal surface of the mandibles; maxillary palp mostly without pigment except for the light pigmentation along the dorsal surface of the 3rd article; labial palp with line of purple pigment along the outer margin of the penultimate article. Pronotum with light pigment patchily over disk, becoming denser towards the anterolateral margins; meso- and meta-nota with very little pigment being only visible in the anterolateral region. Prosternum with conspicuous rectangular area of dark pigment posterior to the submedial combs of macrochaetae (except for between the combs), meso- and meta-sterna with oblique lines of pigment arising just posterior to the submedial combs angled towards the mid-line; pro- and mesosternum also with transverse line of dark pigment adjacent to the following segment. Coxa of all legs with blotchy purple pigment on inner anterior corners, trochanter without pigment, femora and tibia of all legs with pigment along the ventral line of strong macrochaetae and over much of dorsal surface. All urotergites pigmented in middle 50% with the pigment becoming darker towards the posterior margin of each urotergite, the degree of pigmentation of each segment is progressively stronger towards the posterior end; urotergite X darker especially along posterior margin, styli pigmented or more strongly sclerotized apically; ovipositor with light pigment along the mid-ventral surface of the anterior gonapophyses.

Macrochaetae: Smooth, apically bifid but bifurcations distinctly truncate even in smaller setae of antennae (Figs 2, 8), some appear to be apically trifurcate while others have a double bifurcation (Fig. 3) and others quite flattened apically although still bifurcate; light brown in colour. Some carrot-shaped macrochaetae on legs (Fig. 9). Many smaller setae or chaetic sensilla (Fig. 2) also apically bifurcated but some, especially on the maxillary palp, almost pointed (slightly truncated apically under high magnification). Other setae are simple and lack bifurcation or apical truncation. Macrochaetae are present on the terminal filaments, the pedicel and scape but not on the flagellum of the antennae.

Head: Longer than wide, very flattened and prognathous with the antennal bases positioned well forward (Fig. 10); chaetotaxy well developed, anterolateral corners of frons with 1+1 bushes and a groove between them, the sides of which showed dark pigment when the specimen was in alcohol but which completely faded when slide mounted; behind these anterior groups there is a small gap before a short lateral group about two macrochaetae wide with 1+1 (or 1+2) isolated macrochaetae behind them (possibly homologous with the peri-antennal group of Lepismatidae) followed by a much longer gap to a small group of macrochaeta at the anterior corner of the eyes and another group on the margin behind the eyes and a stout carrot-shaped macrochaetae posterolaterally. Disc of head with scattered cilia. Clypeus difficult to see in slide mounted material but appears to have 1+1 proximal rows of strong macrochaetae, longer than those on the frons. Labrum with numerous long macrochaetae, two long thin setae and several cilia. Eyes dark, not prominent, composed of 12 ommatidia. — Antennae (Figs 4, 5, 11, 12) quite long and densely covered in apically bifurcate setae, scape longer than wide with subapical ring as well as four groups of strong setae in shorter (two setae) or longer (several setae) rows across the dorsal outer face, pedicel about as long as wide and only about half the length of the scape, with subapical ring of shorter strong setae and some very long macrochaetae. Limits between annuli of the flagellum are in some cases difficult to discern with a light microscope, but more evident with SEM, where they can be identified by the wrinkled integument (Fig. 5). Six basal annuli of the flagellum each with one ring of setae and several trichobothria; in the first one, some trichobothria are inserted below the ring of setae showing the zone where the basal growth of the antennal flagellum originates. From the seventh annulus, each one has two rings of setae, but in the section between the 10th and the 30th some annuli have three rings, and in the apical part (more distal than the 100th annulus) the annuli bear only one ring of setae. When more than one ring appears in an annulus, they are closely positioned in the basal part of the antenna and more separated in the apical part. All basal annuli have trichobothria. The first annulus without these sensilla is the 14th. The number of annuli forming an interval increases towards the apex (three from annuli 26–28 and four from 44–47), to the point that most apical surviving intervals (Fig. 12) consist of 16 annuli. A high diversity of sensilla has been detected using the SEM; most of these are difficult to see with light microscopy, not only because of their small size, but also because of the similarity of some of these types with low magnification

Figure 2. *Maindronia bashagardensis* sp. nov. holotype ♀, chaetic sensilla of antenna.

Figure 3. *Maindronia bashagardensis* sp. nov. holotype ♀, apex of double bifurcate macrochaeta.

and the fact that the high density of setae, all somewhat laid flat on the slide, makes examination of these structures difficult. Trichoid sensilla (cilia) are visible from the fifth annulus. A type of thin seta with bent base is present from the fourth annulus. At least four types of basiconic sensilla are present; three of them can be attributed to the types A, B and C described by Adel (1984). Some other types of sensilla are present, such as campaniform (usually associated with T-annuli) and dome-like sensilla that can considered as equivalent to coeloconic type. Rosette-like structures, like those described by Matushkina (2010), have also been observed in several annuli. The distribution pattern of these types of sensilla is very regular along the antenna. For example, a pair basiconic A - basiconic C is usually present in the same position of the antenna in each interval below the T-annulus (in the penultimate annulus of the interval when the interval consists of three or four annuli). — Mandibles (Figs 13, 14) quite large with a well-developed incisor region but lacking a molar region, a line of 11 shorter and six longer apically bifurcate setae along the distal ventral

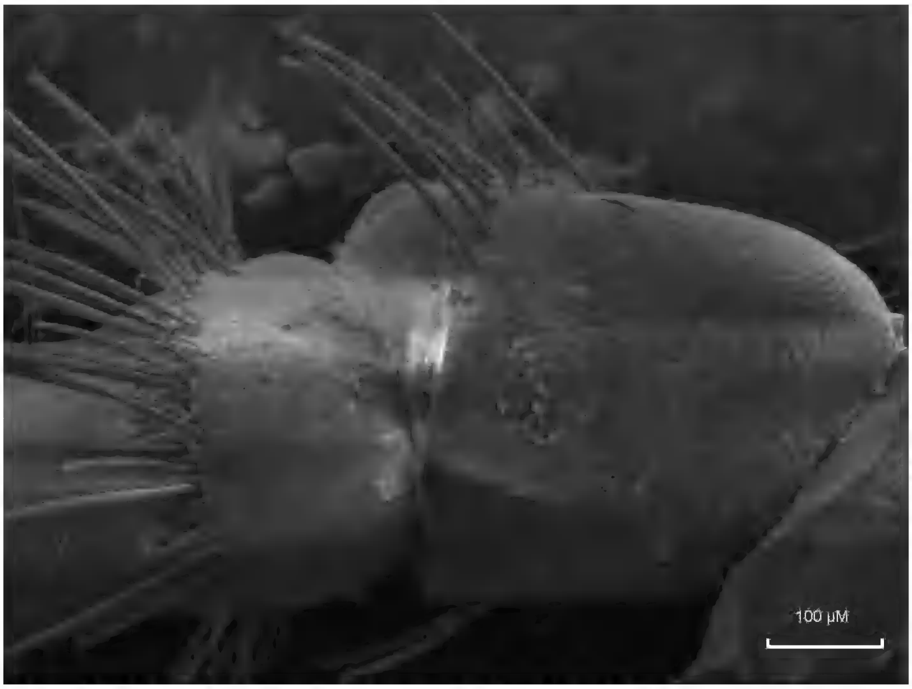
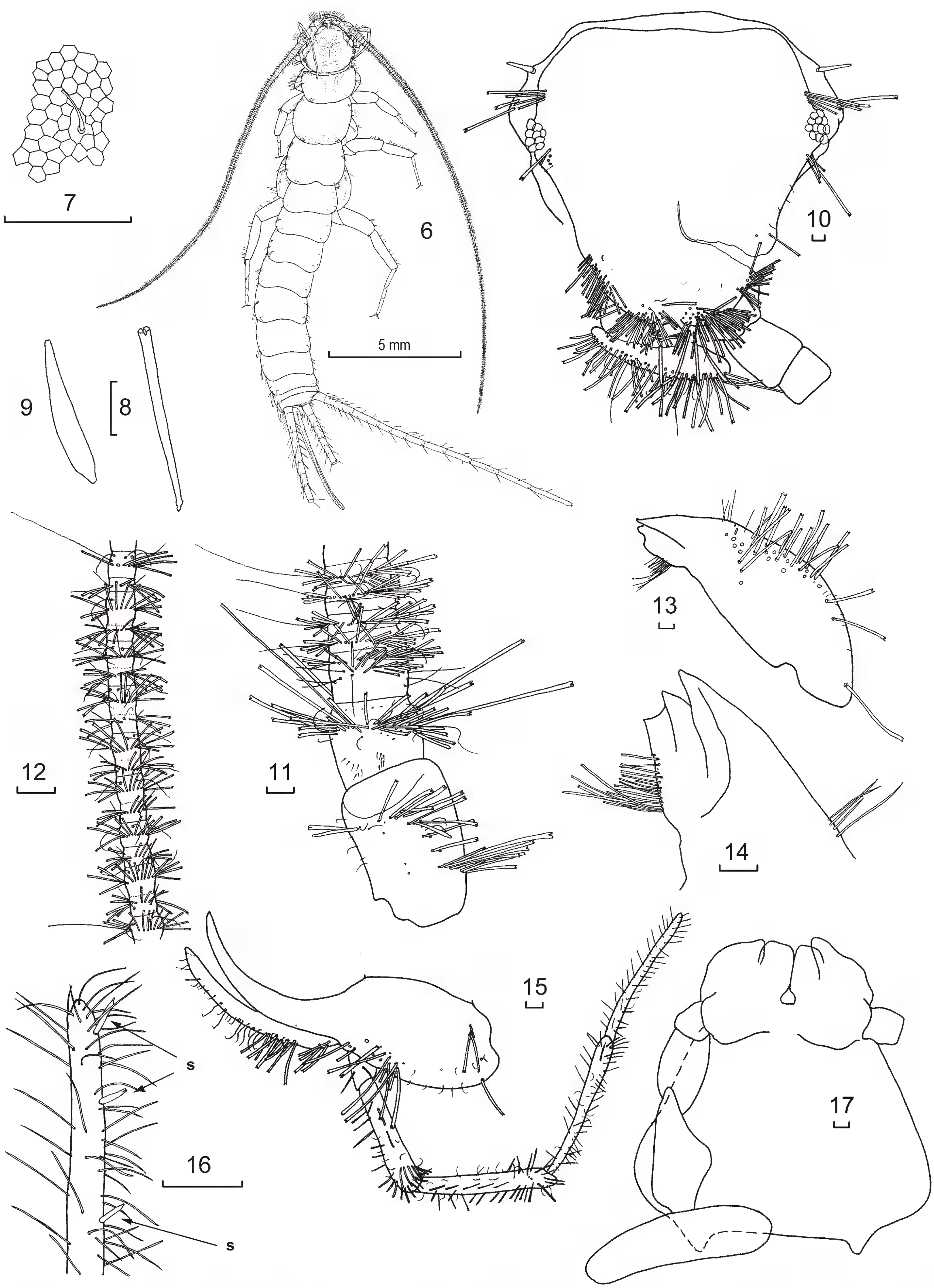


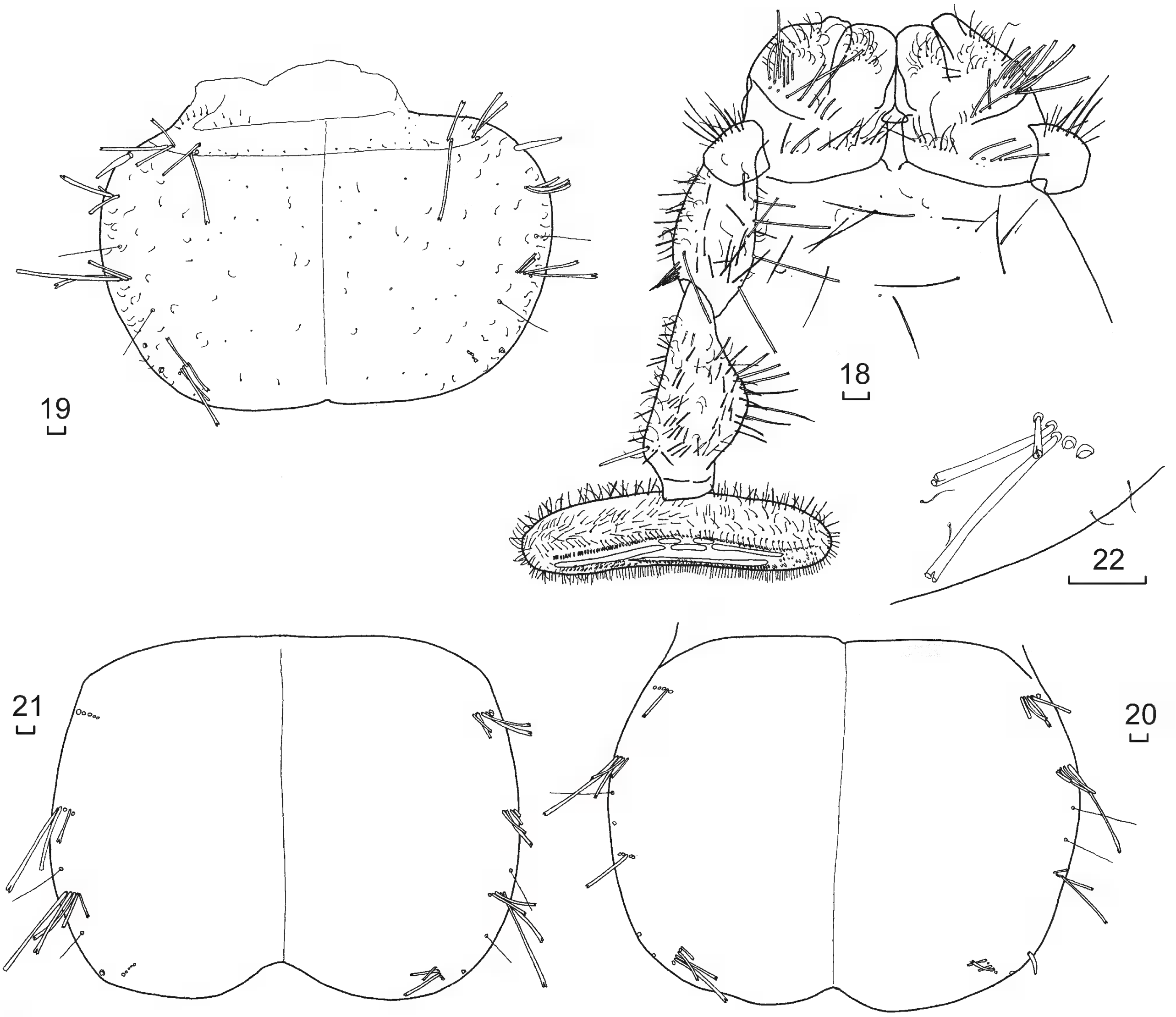
Figure 4. *Maindronia bashagardensis* sp. nov. holotype ♀, pedicel and scape of antenna.

Figure 5. *Maindronia bashagardensis* sp. nov. holotype ♀, wrinkled integument of the area limiting two consecutive annuli of the antennal flagellum.

margin proximal to the incisor region and a bush of 30+ macrochaetae externally. — Maxilla (Figs 15, 16) laterally quite prominent with several strong macrochaetae and cilia as in Fig. 15, with a very simple curved lacinia, which is a little longer than the slender galea, apex of galea without apical lobes, instead having a "chiselled-off" appearance like rodent teeth (on both left and right sides so probably not an injury), galea also with some stronger macrochaetae basally. Palp very long and slender, the apical article about 17 times longer than wide and similar in length to the penultimate article, basal article small with just a couple of bifurcated setae, second, third and fourth articles long with more numerous bifurcated setae and long cilia, especially around the distal end of each article, ultimate article quite thin, with three large papillae in the distal quarter, these resemble a large curved basiconic sensillum (type C of Adel, 1984) but with one or two apical papillae (Fig. 16). — Labium (Figs 17, 18) only very slightly longer than broad, postmentum very long with all setae confined to the distal half; prementum between palps with transverse row of cilia



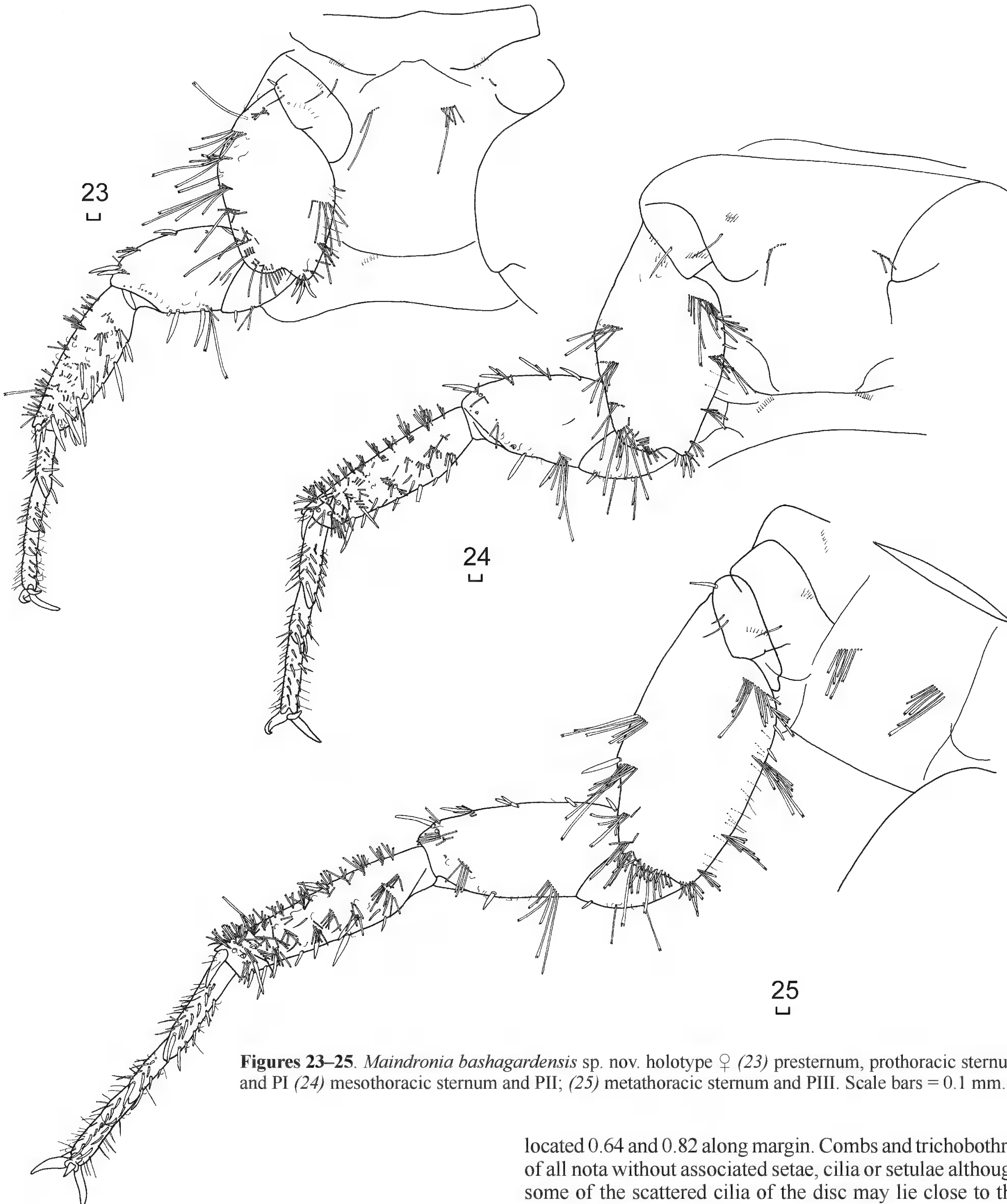
Figures 6–17. *Maindronia bashagardensis* sp. nov. holotype ♀ *(6)* habitus, caudal filaments incomplete; *(7)* tessellated cuticle surface of vertex, with typical tiny scattered seta; *(8)* smooth, apically bifurcate macrochaeta of frons; *(9)* carrot-shaped macrochaeta of tibia PIII; *(10)* head; *(11)* antenna, scape, pedicel and basal intervals of flagellum; *(12)* idem, most distal surviving interval; *(13)* mandible; *(14)* idem, enlargement of apex; *(15)* maxilla; *(16)* idem, ultimate article of palp with three sensilla (s); *(17)* labium, outline only. Scale bars = 0.1 mm unless otherwise indicated.



Figures 18–22. *Maindronia bashagardensis* sp. nov. holotype ♀ *(18)* labium, anterior half, and palp, showing chaetotaxy; *(19)* pronotum; *(20)* mesonotum; *(21)* metanotum; *(22)* idem, right posterior comb. Scale bars = 0.1 mm.

and setae, those laterally are bifurcated, paraglossae with oblique row of macrochaetae as well as a loose lateral bush of several macrochaetae and a row of weaker setae along the outer margin, apices of paraglossae and glossae with long cilia (Fig. 18); palps about the same length as labium, articles one to three with long bifurcated macrochaetae as illustrated (Fig. 18), apical article subrectangular, almost sausage-shaped and very wide being almost four times as wide as long, with a long anterior papilla of the aufgelöst type in the middle but becoming more compact towards each end, then something that resembles the 3+2 arrangement in many lepismatid genera although the two outer papillae in the more anterior row are also very long and the individual units of the papillae more compacted together; these papillae are fringed with a line of rod-like structures, the rest of the segment covered with numerous setae (some quite stout), no other specialized sensilla observed.

Thorax: Only slightly wider than head or abdomen, subparallel sides, the surface of all nota with scattered cilia, these being more numerous near the lateral margins. Pronotum (Fig. 19) only slightly wider than head (1.08) with slightly indented posterior margin; anterior margin without setal collar but with scattered cilia along the entire margin, lateral region of anterior margin with two groups of three macrochaetae on each side, lateral margin with a stout slightly carrot-shaped macrochaeta in the anterior corner, followed by a comb of three macrochaetae then an isolated trichobothrium slightly anterior of halfway (0.40 of total margin length along margin), followed by a comb of four or five macrochaetae, followed by another trichobothrium (0.62 along margin) followed by one or two presumably stout macrochaetae closer to the margin and an oblique comb of five macrochaetae, the trichobothria and the combs in the posterior half are much more distant from the margin than is usually observed in the Lepismatidae; posterior margin glabrous. — Mesonotum (Fig. 20) also with numerous scattered cilia over the surface (not illustrated) with the most anterior comb consisting of five macrochaetae, the following comb of four macrochaetae followed by a trichobothrium (0.44 along margin), and another trichobothrium (0.52 along margin), followed by a comb of five macrochaetae,

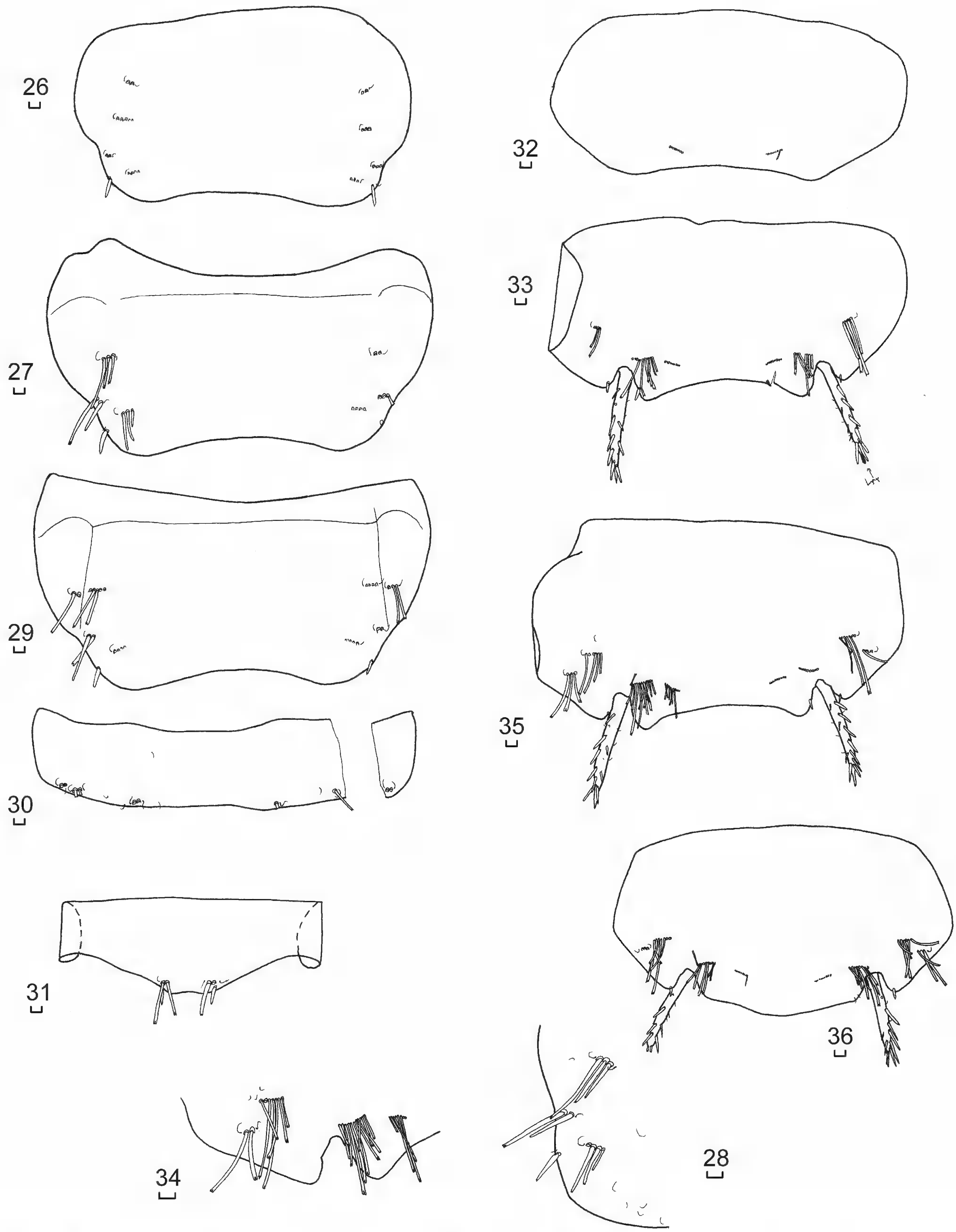


Figures 23–25. *Maindronia bashagardensis* sp. nov. holotype ♀ *(23)* presternum, prothoracic sternum and PI *(24)* mesothoracic sternum and PII; *(25)* metathoracic sternum and PIII. Scale bars = 0.1 mm.

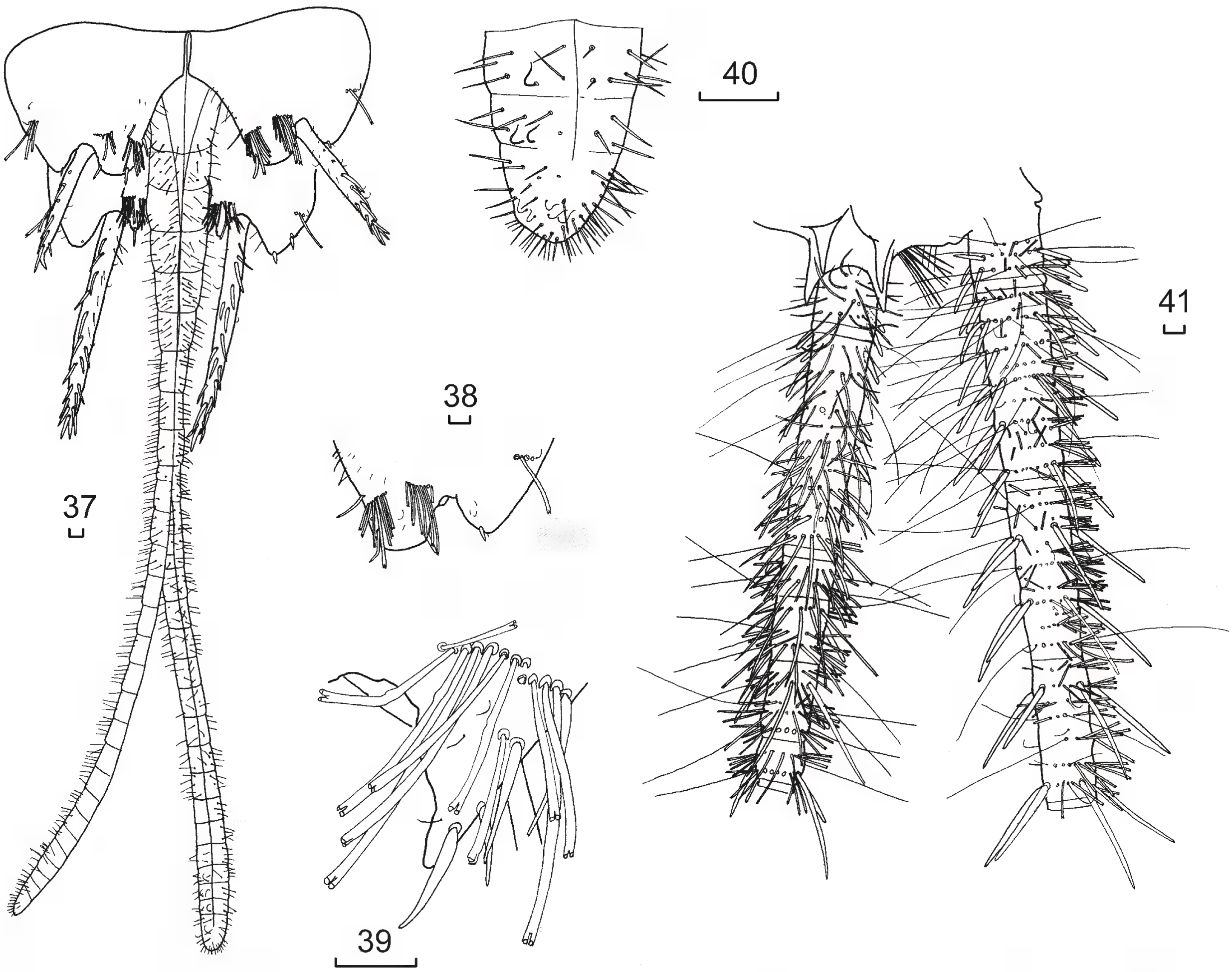
then two (presumably) carrot-shaped macrochaetae on the margin at close to the level of the oblique posterior combs, these combs consist of six macrochaetae which become progressively larger posteriorly; the posterior margin with a very pronounced concavity medially. — Metanotum (Fig. 21) similar to mesonotum, with three combs on each side with five, four and five macrochaetae, each posterolateral corner with only one marginal macrochaeta, oblique posterior combs of five macrochaetae (Fig. 22), the trichobothria are located 0.64 and 0.82 along margin. Combs and trichobothria of all nota without associated setae, cilia or setulae although some of the scattered cilia of the disc may lie close to the combs or trichobothria.

Presternum of prothorax ill-defined in slide material but glabrous (Fig. 23). — All thoracic sterna not free (Figs 23–25) with a large exposed area between the coxae, with 1+1 combs each of 6–10 macrochaetae adjacent to the precoxae.

Legs quite long (Figs 23–25), becoming progressively longer posteriorly with the tibia of PI only 0.64 the length of tibia of PIII and the tarsus of PI only half the length of the tarsus of PIII; tibia L/W ratio of legs PI 3.5, PII 3.3, PIII 4.1; tarsi L/W ratio PI 8.0, PII 8.6, PIII 13.7. — Precoxa of prothorax with a line of five macrochaetae, the most



Figures 26–36. *Maindronia bashagardensis* sp. nov. holotype ♀ *(26)* urotergite I; *(27)* urotergite III; *(28)* idem, left lateral side; *(29)* urotergite IV; *(30)* urotergite IX (in two pieces); *(31)* urotergite X; *(32)* urosternite II; *(33)* urosternite III; *(34)* urosternite IV, detail of right posterior side; *(35)* urosternite V; *(36)* urosternite VII. Scale bars = 0.1 mm.



Figures 37–41. *Maindronia bashagardensis* sp. nov. holotype ♀ *(37)* coxites VIII and IX, styli and ovipositor; *(38)* combs of coxite VIII, left side; *(39)* inner process of coxite IX, right side; *(40)* apex of ovipositor; *(41)* base of cercus and median dorsal appendage. Scale bars = 0.1 mm.

lateral being carrot-shaped as well as an isolated simple macrochaeta. — Coxae of all legs with several combs of up to ten macrochaetae along or near the lateral margin as well as some thicker isolated macrochaeta (three on PI, one on PIII), inner margin with three to six combs, the more proximal consisting of two combs close together, combs of up to thirteen macrochaetae as illustrated, with at least three strong and several smaller macrochaetae over the articulation with the trochanter. — Trochanter of all legs with two slender macrochaetae and one short carrot-shaped macrochaeta. — Femur with isolated stout macrochaetae along anterior margin proximally, then two or three similar macrochaetae about midway, distal quarter with two combs each of up to nine macrochaetae some of which are carrot-shaped. Posterior margin of femur with up to three long carrot-shaped macrochaetae and a proximal comb. — Tibiae all with several stout carrot-shaped macrochaetae as well as mostly shorter, more slender, macrochaetae formed into numerous combs over the ventral face and anterior margin as illustrated, the carrot-shaped macrochaetae sometimes incorporated into the combs of thinner macrochaetae, apical spine with some small setae and a cilium. — Tarsus with four articles, the basal article on PI being about one third the length of the tarsus and two fifths on PIII, all tarsal articles with short carrot-shaped macrochaetae along the ventral surface and simple setae on the dorsal surface. — Pretarsus with long thick fairly straight outer claws that narrow and curve apically, medial empodial claw smooth and short.

Abdomen: Urotergite I (Fig. 26) with 4+4 combs of 2–5 macrochaetae each comb with and one or two cilia, as well as 1+1 carrot-shaped macrochaetae near the posterolateral corners. Urotergites II–III (Figs 27, 28) with 3+3 combs (missing the more anterolateral comb) as well as 1+1 carrot-shaped macrochaetae near the posterolateral corner; the redundant suture with the paratergites is vaguely visible on tergites IV–VIII (Fig. 29). Urotergites V–VIII with 4+4 combs as well as 1+1 carrot-shaped macrochaetae on the posterolateral corner. Urotergite IX (Fig. 30) with 3+3 posterior combs fairly close to the margin, the most lateral composed of two macrochaetae, the sublateral of 1–2 macrochaetae and the submedial of 1–2 macrochaetae, each comb with one or two cilia adjacent to the comb, when only one, this is usually lateral of the comb; medial region with irregular pigment — Urotergite X (Fig. 31) short, trapezoidal, with 1+1 submarginal combs of two macrochaetae on the apices and a single, carrot-shaped macrochaeta on the posterior margin adjacent to the combs,

Table 1. Number of macrochaetae in each bristle comb.

	urotergites				urosternites			
	anteromedian	anterosublateral	posterolateral	posteromedian	posterolateral	lateral	sublateral	submedial
I	2	3–5	2–3	3–4	—	—	—	—
II	—	4	2	4	—	—	—	8
III	—	2–3	2–3	3–4	—	4	11–12	9–10
IV	4–5	2–3	2	4–5	3	4	11	8
V	2–3	3	2	3–4	3	6–7	11	10
VI	2	3–4	2	3–4	3–4	6–8	10–11	8–9
VII	2–3	3–5	2	4	3	6–7	11	9–10
VIII	2	2–3	2	3	3–4	—	7–10	5
IX	2	1–2	—	1–2	3	—	9–10	7–8

each comb associated with cilium lateral of the comb, the surface with a few scattered curved setulae, the medial area with pigment which is darker along the posterior margin, the posterior margin between the combs somewhat concave.

Urosternite I glabrous. Urosternite II (Fig. 32) with 1+1 submedial combs well anterior of the margin. Urosternites III with 3+3 combs (lacking the most lateral) (Fig. 33). Urosternites IV–VII (Figs 34–36) with 4+4 combs with two combs laterad of the styli and two mediad of the styli, the most lateral comb on II–VIII with 3–4 macrochaetae as well as a cilium laterad of the comb, the sublateral combs with 4–8 macrochaetae and rarely a cilium laterad of the comb, the lateral combs (mediad of the styli) with 7–12 thinner macrochaetae, the submedial combs with 8–10 thinner macrochaetae, often (but not always) with a small carrot-shaped macrochaetae near the margin on either side of the stylet insertion and sometimes another laterad of the stylus. Coxites VIII in ♀ (Figs 37, 38) separated into two coxites each with three combs as well as five short carrot-shaped macrochaetae along the margins, one near the apex of the rounded outer process, two on either side of the rounded inner process and two more along the inner margin of the inner process; the lateral comb of 3–4 macrochaetae and a laterad cilium, the other two combs are at the base of the inner process, the comb adjacent to the stylus with 9–10 macrochaetae, the submedial combs of 7–8 macrochaetae.

Coxite IX in ♀ (Figs 37, 39) with a small lateral comb of three macrochaetae associated with a laterad cilium, and three combs quite close together on the internal process, the more lateral being slightly anterior to a smaller comb adjacent to the ovipositor and another smaller comb more posterior, apices of both inner and outer processes with one or two marginal, carrot-shaped macrochaetae.

Styli (Fig. 37) present in seven pairs i.e. on urosternites III–IX, those on IX being about 1½ times longer than those on VIII. All styli with terminal spines similar to that observed in the Nicoletiidae as well as several stout almost carrot-shaped macrochaetae along the shaft of each stylus.

Ovipositor (Figs 37, 40) of primary type, moderately long (1.1 times HW), surpassing the apices of the styli by about twice their length, with 28–29 divisions, each division especially those apically with small conical setae.

Epiproct and paraprocts not strongly pigmented or sclerotized (Fig. 41), both appearing as very sharp processes over the base of the median dorsal appendage. — Cerci (Fig. 41) incomplete, basal division short, about as long as wide, with three rings of setae, macrochaetae and trichobothria, pronounced joint to next division; second division about three times longer than wide, with six rings of strong macrochaetae as well as secondary rings of smaller setae and trichobothria between them; third division similar but with only four rings of strong macrochaetae, setae, long trichoid sensilla and trichobothria as well as about thirteen secondary rings, this division subdivided by faint suture a bit beyond half way; following three divisions only half as long with only two rings containing stronger macrochaetae, as well as several secondary rings. — Median dorsal appendage (Fig. 41) incomplete (>0.17 H+B) with basal division a little longer than wide with about four rings of simple or apically slightly bifurcate setae as well as strong slightly bifurcate carrot-shaped macrochaetae on each side of the more distal rings, the joint between this and the following segment very prominent appearing almost as a separate and slightly wider segment, the second division much longer (about four times longer than wide) with six rings of stronger setae including the lateral carrot-shaped macrochaetae as well as four rings of smaller apically-bifurcate setae between the more distal rings of larger setae and several long trichobothria, again with a prominent joint between this and the following division, the third division of similar length and chaetotaxy but with three subtle suture lines, dividing the division into four subunits, the basal and the most distal each with one ring of strong macrochaetae, the middle two each with two rings of stronger seta, all subunits with additional rings of smaller setae and many long trichobothria.

Male unknown.

Biology. The specimen was collected on tiles within a home.

Discussion

The Maindroniidae are not well known, with only four descriptive publications, the most recent by Schremmer in 1964, a time when the importance of trichobothria and specialized sensilla for lepismatid taxonomy was not recognised. Details of the chaetotaxy were also very cursory. This paper addresses some of the characters below but no doubt there is still much more to be learned.

The **macrochaetae** of *Maindronia bashagardensis* sp. nov. are referred to as smooth (although their surface structure is distinctly corrugated) and apically bifurcate and quite distinct from the barbed or pectinate macrochaetae seen in some lepismatid families. They are somewhat similar to the macrochaetae in *Heterolepisma* Escherich and *Anisolepisma* Paclt. Apically bifurcate macrochaetae appear throughout all known zygentoman families and are probably plesiomorphic as proposed by Mendes (1988).

The **head** has 1+1 bushes of macrochaetae in the anterolateral corners of the frons similar to those seen in several Lepismatidae. The clypeus appears small and with a few macrochaetae. The labrum is very wide and has numerous macrochaetae, more similar to the Lepismatidae than other families.

The **mouthparts** of the species are strikingly different to the other four extant families of the Zygentoma. The very prognathous and elongate head, the pincer-like laciniae and the apparent absence of a molar region of the mandibles, suggest a predatory behaviour (Koch, 2003). Schremmer (1964) reported on the extreme agility of *M. beieri* which suggests they have the speed and dexterity to pursue prey, although most Zygentoma are quite rapid in their escape behaviour. However, Zúñiga-Reinoso & Predel (2019) suggest otherwise due to the total absence of metameric prey in the hyperarid areas of the Atacama Desert from which numerous *Maindronia* specimens were collected.

The **maxillary palps** are extremely elongate, even more so than seen in troglobitic Nicoletiidae. The last segment has three sensilla in the same locations as seen on Heterolepismatinae Mendes, 1991, but the sensilla do not have multiple "arms" but just one or two apical papillae.

The last article of the **labial palp** of *Maindronia bashagardensis* sp. nov. is flat and extremely widened. The anterior margin has papillae in a 1+3+2 arrangement, the first distal papilla being very long, as are the two outer papillae in the next row. The individual units of the distal papilla are more widely spaced (aufgelöst) in the centre, but closer together in other parts. The other 3+2 papillae have the individual units more closely packed. The region occupied by all papillae is fringed with a row of stout rod-like structures of unknown function. While some similarity can be seen with arrangements in the Nicoletiidae (3+2+1) and many Lepismatidae (3+2) the arrangement in *Maindronia* is unique and offers little evidence of relationships. Six papillae in three lines may be the more ancestral condition.

The **nota** of *Maindronia bashagardensis* sp. nov. are not wide. The anterior margin of the pronotum lacks a setal collar but has a line of small cilia, similar to those over the rest of the surface of the nota. There are 2+2 groups each of three macrochaetae distally, which may perhaps be homologous with the isolated groups seen in a similar position of some Acrotelsatinae (e.g., *Anisolepisma* spp.).

All nota of *Maindronia bashagardensis* sp. nov. have submarginal combs, similar to many Lepismatidae. All nota also have two trichobothria on each side, suggesting a closer relationship to the Lepismatidae than the other families. The nota (and urotergites) uniquely have 1+1 (or 2) short posterolateral carrot-shaped macrochaetae.

The **thoracic sterna** of *Maindronia bashagardensis* sp. nov. are unlike any Lepismatidae, neither have the free sternum nor the raised medial mound between the coxae. The basic structure is more like that in the Nicoletiidae, Protrinemuridae Mendes, 2002 and Tricholepidiidae Engel, 2006 and should probably be considered as plesiomorphic.

Antennal sensilla display a high diversity in the antennal flagellum of this specimen suggesting a close relationship between the Maindroniidae and Lepismatidae. Most of the types observed by Adel (1984) in *Thermobia domestica* (Packard, 1873) are present in *Maindronia bashagardensis* sp. nov. Common occurrences not only involve the types of sensilla, but even some aspects of their pattern of distribution, for example the constant association of a basiconic A sensillum with a basiconic C, as photographed by Adel (1984, page 201, fig. 20). However some sensorial structures, such as bent-base setae and some types of basiconic sensilla, appear to be exclusive to the Maindroniidae, showing a high degree of specialization. Sensilla in Nicoletiidae are less diverse, suggesting a more plesiomorphic position of this family respect to Maindroniidae. This agrees with the proposal of Koch (2003).

All **urotergites** of *Maindronia bashagardensis* sp. nov. have combs of macrochaetae but unlike those of the Lepismatidae, they are often quite remote from the margins. Combs are absent from the Nicoletiidae, Tricholepidiidae and Protrinemuridae.

Urotergite X is short, trapezoidal with a slightly concave posterior margin, the posterior apices each bearing a short comb of two macrochaetae. Short trapezoidal or weakly rounded shape is seen in most families of Zygentoma and is probably plesiomorphic.

Most **urosternites** have combs with only urosternite I being glabrous. The combs are however much more numerous than seen in the Lepismatidae and positioned over the disc not just near the posterior margin. The common ancestor of the Lepismatidae and Maindroniidae may have had several combs.

The **ovipositor** of the Maindroniidae is simple and similar to several Lepismatidae (e.g., Lepismatinae Latreille, 1802 and Heterolepismatinae). It lacks the field of small curved "hooks" seen in the ovipositor of the Nicoletiidae and is therefore probably more closely related to the Lepismatidae than the other families.

It appears that the Maindroniidae, while having thoracic sterna similar to the Nicoletiidae, share many more characters with the Lepismatidae and are probably a sister group. Their current disjunct distribution (Middle East and South America) supports the view that they are an ancient relic group.

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